Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

The vegetation of Connecticut

V. Plant societies along rivers and streams*

GEORGE E. NICHOLS

(WITH ELEVEN TEXT FIGURES)

In the present series of papers on the vegetation of Connecticut, the principle of succession has been adopted as the most satisfactory basis for classifying plant associations. This scheme of classification, it may here again be remarked, treats vegetation both from a genetic and a dynamic standpoint. It recognizes the fact that plant societies, or associations, as they exist today, are the product not alone of contemporaneous conditions, but of past conditions as well. It also emphasizes the fact that the plant associations of today are not necessarily permanent, but are liable to change through the influence of various factors.

In the third and fourth papers of the series,† attention was directed to the plant associations of uplands and of lowlands. There the changes in vegetation, and therefore the succession of plant associations, are influenced primarily by plant and animal agencies—in other words, by biotic factors. There remain to be considered, then, successions which are associated not only with biotic factors but with topographic factors as well. Succession of this sort has been termed TOPOGRAPHIC SUCCESSION. Topographic succession is seen principally along rivers and streams and along the coast. The present paper deals with plant societies along rivers and streams. Some of these societies might almost equally well have been treated along with the societies of uplands and of lowlands; yet, on the whole, so marked may be the impress of a stream on the vegetation at its margin, and so closely linked may be the development of the one with that of the other that the two cannot well be treated separately.

---

* Contribution from the Osborn Botanical Laboratory.

† Torreya 14: 167–194. 1914; Bull. Torrey Club 42: 169–217. 1915.

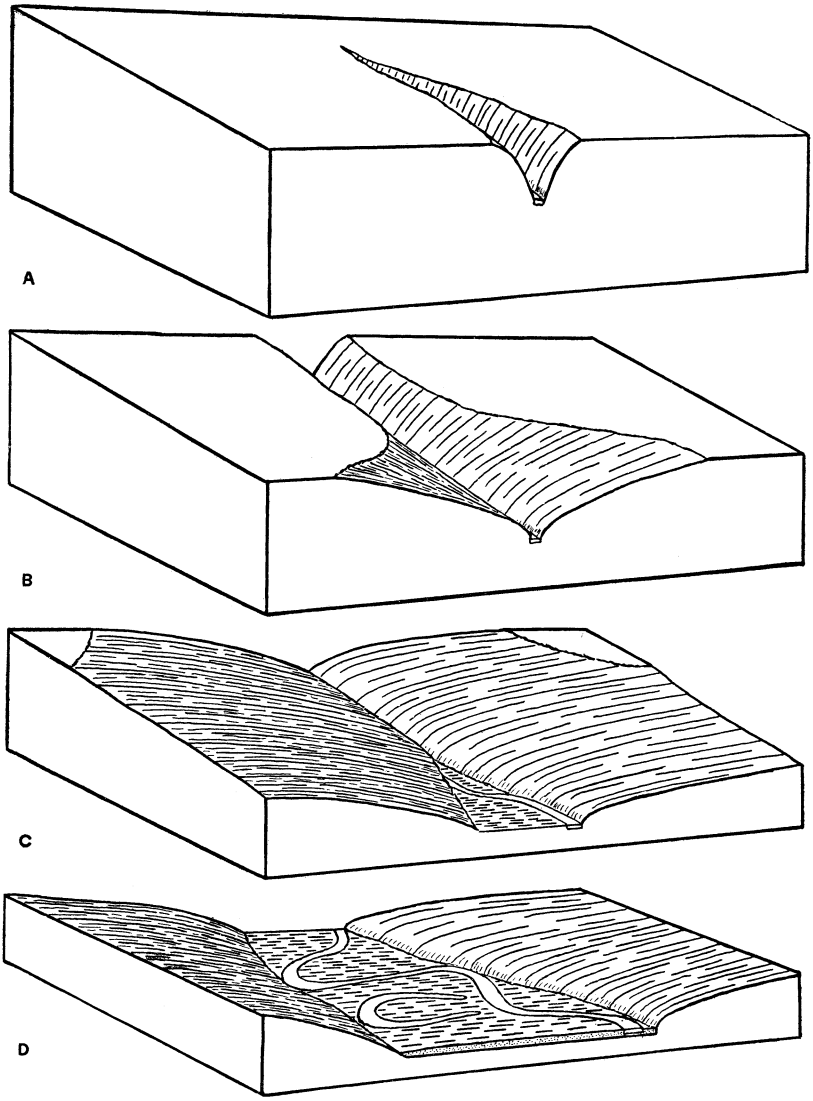

FIG. 1. Diagrams showing various stages in the development of a river.

THE LIFE HISTORY OF A RIVER

Various stages in the life history of a river are graphically represented in FIG. 1. In a young stream the current is swift and wears away the floor and sides of its channel. Vertical erosion, however, is greater than lateral, so that the stream may gradually intrench itself in a narrow ravine or canyon. At this stage of stream development vegetation is largely confined to the flanks of the ravine. During the course of time, as the channel is cut deeper and deeper, downward erosion proceeds more and more slowly, ultimately ceasing altogether, while lateral erosion becomes correspondingly more pronounced; so that, as the stream approaches maturity, it comes to occupy a broad valley which it has carved out for itself. Vegetation covers both the bordering bluffs and the floor of the valley. As the level of the stream approaches the level of the water at its mouth, the current becomes sluggish and aggradation largely succeeds degradation. An old age river meanders about in broad, sweeping curves on the flood plain which it has built up out of sediment derived from younger parts of its system. A very distinctive type of vegetation is developed on flood plains.

Of course, the rate at which the topographic changes outlined in the preceding paragraph are effected varies widely according to the nature of the rock formations concerned. The scouring out of a ravine in clay or gravel, for example, may proceed with comparative rapidity, but the erosion of a ravine in rock is extremely slow. Ravines in glacial till and outwash have been developed since the retreat of the glaciers, and may even now be observed in the process of active formation. In most rock ravines, on the other hand, the topographic changes since the ice age have been practically negligible. The bearing of these facts on the nature of the vegetation will be referred to in later paragraphs (pp. 245, 249).

ROCK RAVINES

Occurrence and General Features.—Throughout the region under discussion the rock ravine is the common type. It abounds in the highland districts, and in the Central Lowland is frequent along the trap ranges and elsewhere. Owing mainly to the nature of the rocks concerned, canyons with overhanging or perpendicular walls are absent. The predominant type of rock ravine (FIG. 2) is somewhat V-shaped in cross section, often narrow and precipitous below but broadening out above. Toward the bottom the vegetation may be restricted to such forms as can cling to the rock face or maintain a foothold in crevices, but higher up the sides are usually forested.

There are, of course, all sorts and sizes of ravines. In the remarks on the nature of ravine vegetation which follow, the writer has in mind a number of unusually good examples, such as Sage's Ravine and the Wolf Den in Salisbury, the Glen along Spruce Brook at Beacon Falls, Wintergreen Falls ravine in

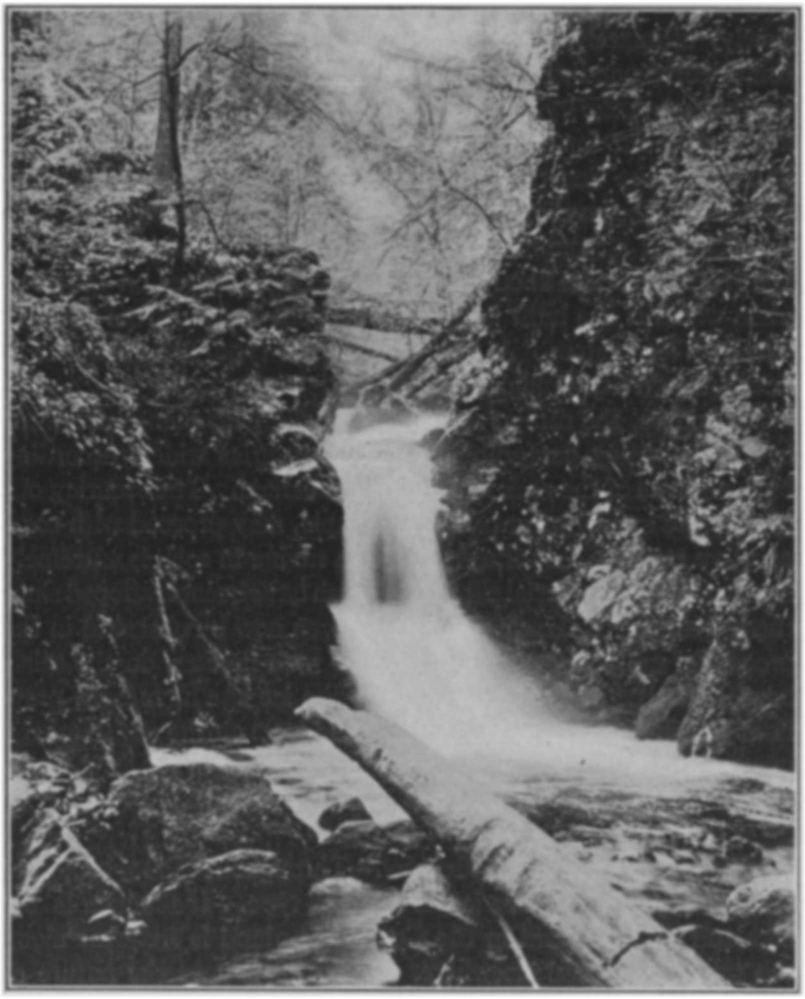

FIG. 2. Precipitous rocky slopes along stream in Sage's Ravine, Salisbury. The cliffs in the foreground are covered with mosses and liverworts.

Hamden, Woodbridge Glen in Woodbridge, Roaring Brook ravine in Cheshire, Devil's Gulch in Branford, and Ninevah Falls ravine in Killingworth. Most of these are ravines of considerable depth and have a good-sized brook at the bottom. To shallower, less well-developed ravines the remarks naturally may not be equally applicable.

The Bryophytic Flora of Rock Ravines.—Perhaps the most striking feature of the vegetation near the bottom of a ravine (FIG. 2) is the rich display of mosses and liverworts. In the stream itself, attached to rocks but always submerged, grow various aquatic forms, such as *Fontinalis*. Other more or less hydrophytic species cover the low-lying, wet and frequently submerged rocks along the margin and in the bed of the stream, mantle the spray-dashed rocks at the foot of waterfalls, and form extensive mats even in rapids and similar precarious situations. The following more or less hydrophytic species may be looked for in such places:

Chiloscyphus rivularis
Scapania undulata
Porella pinnata
Fontinalis dalecarlica
Fontinalis gigantea
Fontinalis Lescurii
Oxyrrhynchium rusciforme
Amblystegium fluviatile
Amblystegium irriguum
Hygrohypnum dilatatum
Hygrohypnum eugyrium
Hygrohypnum ochraceum

Growing on periodically inundated rock surfaces, either in the bed of the stream or along its sides, are such forms as *Fissidens incurvus*, *Grimmia apocarpa*, *Racomitrium aciculare*, and *Brachythecium plumosum*. Along with these, but usually on springy banks or on continuously moist rock surfaces, where they may or may not be submerged during flood time, may occur:

Conocephalum conicum
Pellia epiphylla
Plagiochila asplenioides
Lophocolea bidentata
Jubula pennsylvanica
Anthoceros laevis
Fissidens adiantoides
Mnium hornum
Mnium punctatum
Philonotis fontana
Thuidium delicatulum
Brachythecium rivulare
Climacium americanum
Catharinaea undulata

Higher up on the slopes, numerous species thrive in the crevices or plaster the faces of overhanging cliffs and precipitous rocks. The following are fairly characteristic of wet or moist cliffs:

Marsupella emarginata
Plagiochila asplenioides
Scapania nemorosa
Radula complanata
Lejeunea cavifolia
Hymenostylium curvirostre
Didymodon rubellus
Anoectangium Mougeotii
Plagiopus Oederi
Plagiothecium denticulatum
Hylocomium brevirostre
Thamnium alleghaniense

Inhabiting the drier cliffs, either in crevices or on the rock face, are such forms as:

Metzgeria conjugata
Cephaloziella Hampeana
Porella platyphylloidea
Leucolejeunea clypeata
Frullania Asagrayana
Rhabdoweisia denticulata
Grimmia conferta
Ulota americana
Bartramia pomiformis
Hedwigia albicans
Neckera pennata
Haplohymenium triste
Anomodon attenuatus
Anomodon rostratus

The Influence of the Chemical Nature of Rocks on the Distribution of Bryophytes.—In earlier papers of this series* brief reference has been made to the influence of the chemical composition of the substratum on vegetation. In glaciated regions like Connecticut, where most soils are transported and residual soils are rare, this influence is nowhere seen to better advantage than in ravines and similar localities where there are exposures of bare rock. In Connecticut, the problem as to the effect of the chemical nature of the substratum on vegetation concerns chiefly calcareous versus potassic rocks. The granites, gneisses, schists and sandstones, which comprise the bed rock over much of this state, are for the most part rich in potassium, which is one of the principal constituents of orthoclase feldspar and of mica (muscovite and biotite). Calcium also, as one of the components of plagioclase feldspar, hornblende, and certain other minerals, is present in some of these rocks, and in the sedimentary formations—the sandstones and shales—small amounts of calcium carbonate may be included in the cementing material. But, except locally, the amount of lime in these rocks, in so far as it affects vegetation, appears relatively insignificant. The important lime-bearing formations of Connecticut are trap and marble. The former contains potassium in small amount, one or two per cent.; the latter contains none. Trap outcrops (diabase and basalt) occur chiefly in the Central Lowland. The marble (sometimes referred to as a limestone or dolomite) forms extensive deposits in the western part of the state, particularly in the upper Housatonic Valley.

---

* See Torreya **13**: 109, 110. 1913; **14**: 185. 1914.

Owing to their frequently intimate association with rock surfaces, no group of plants, with the possible exception of the lichens, is better qualified to demonstrate the influence of the chemical composition of the substratum on vegetation than the bryophytes. To be sure, many mosses and liverworts apparently flourish indiscriminately on any sort of rock substratum, provided only that requisite conditions of moisture and shade are present. But a large number of species undoubtedly "prefer" either calcareous or potassic rocks, and some are confined to such substrata. A list is given below of local species which favor calcareous rocks. Nearly all of these are commonest in the marble areas of western Connecticut, and several of them have been collected only there. Some, however, occur also along the trap ranges, while a few are known from other scattered localities.

Grimaldia fragrans
Preissia quadrata
Pellia Fabroniana
Lophozia badensis
Lophocolea minor
Cololejeunea Biddlecomiae
Frullania riparia
Saelania glaucescens
Fissidens cristatus
Cratoneuron filicinum
Hymenostylium curvirostre
Tortella tortuosa
Encalypta contorta
Mnium orthorrhynchum
Plagiopus Oederi
Myurella julacea
Amblystegiella confervoides
Amblystegium noterophilum

The species cited in the next list are reputedly calciphobous (i.e. "lime-avoiding"), and are for the most part restricted to potassic rocks.

Marsupella emarginata
Sphenolobus exsectus
Scapania nemorosa
Scapania undulata
Radula obconica
Andreaea petrophila
Andreaea Rothii
Rhabdoweisia denticulata
Dicranum fulvum
Glyphomitrium incurvum
Racomitrium aciculare
Ulota americana
Pterigynandrum filiforme
Brachythecium plumosum
Sematophyllum carolinianum
Hygrohypnum dilatatum
Hygrohypnum eugyrium

The Mesophytism of the Flora in Rock Ravines.—A rock ravine, more than any other sort of habitat, affords environmental conditions congenial to pronounced mesophytic plants. Seepage water is usually abundant along the sides, there is protection from sun and wind, and the humidity of the air, as compared with the surrounding upland, is high. Certain mosses and liverworts are practically confined to such habitats. In a more arid region than Connecticut the same observation might be made with regard to many of the higher plants, but while it is a familiar fact that in this region as elsewhere the flora of rock ravines includes many of the most extreme shade- and moisture-loving ferns and flowering plants, most of the species present are equally representative of other habitats. Species intolerant of shade are largely excluded. The majority of the forms cited in earlier papers as typical of the climax forest of this region are to be found here, and not a few of the common plants of rock ravines thrive elsewhere in wooded swamps. The following list includes a number of ferns and herbaceous flowering plants which may be considered characteristic of rock ravines, though by no means peculiar to them.

Polypodium vulgare
Phegopteris polypodioides
Asplenium Trichomanes
Asplenium acrostichoides
Aspidium spinulosum
Cystopteris bulbifera
Cystopteris fragilis
Lycopodium lucidulum
Arisaema triphyllum
Smilacina racemosa
Streptopus roseus
Trillium erectum
Laportea canadensis
Pilea pumila
Solidago latifolia
Asarum canadense
Actaea rubra
Caulophyllum thalictroides
Chrysosplenium americanum
Impatiens pallida
Viola cucullata
Viola blanda
Viola rotundifolia
Circaea alpina
Aralia racemosa
Sanicula gregaria
Hydrocotyle americana
Cryptotaenia canadensis
Collinsonia canadensis

The Ravine Forest.—The intense mesophytism of a rock ravine is further accentuated by the nature of the ravine forest (Fig. 3). As a rule the hemlock and yellow birch are prominent, and more often than not they predominate. Along with them commonly occur the sugar maple and others of the trees elsewhere cited as characteristic of the climax forest in this region. The woody undergrowth usually includes *Hamamelis virginiana*, *Kalmia latifolia*, and *Viburnum acerifolium*, while forms such as *Carpinus caroliniana*, *Alnus rugosa* and *Benzoin aestivale*, which one ordinarily associates with swamps, frequently grow along the stream at the bottom. On the whole, ravine forests almost invariably are more mesophytic, and approximate more closely the climax

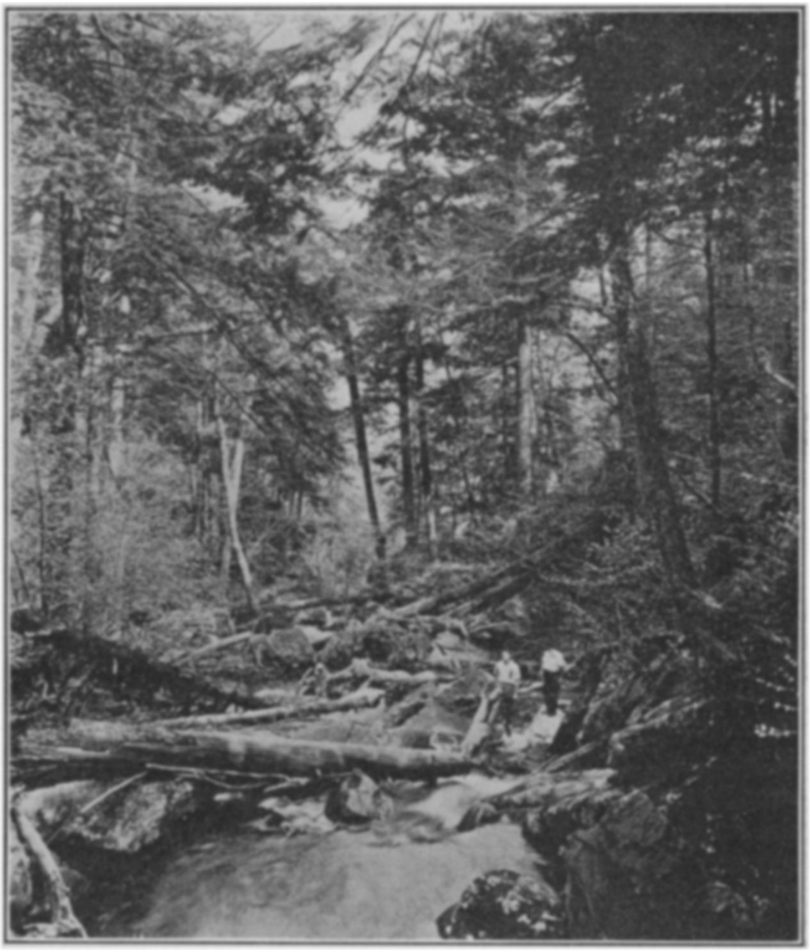

FIG. 3. **Primeval forest in Sage's Ravine. Hemlock and yellow birch the common trees.**

formation of this region than do the forests on the adjoining uplands. In a large measure this fact of course is due to the exceptionally favorable conditions of environment under which they have been developed. But there are other contributory causes which, while they have nothing to do with the development of these forests, may at least be partly responsible for their perpetuation. Thus, on account of their comparative topographic isolation, ravine forests may be largely immune from the fires which frequently devastate the surrounding uplands, while by reason of the difficulty in removing the timber they offer little temptation to the lumberman.

The Boreal Aspect of the Vegetation in Rock Ravines.—A few locally rare Canadian plants, such as *Lophozia alpestris*, *Lophozia attenuata*, *Gymnostomum rupestre*, *Polytrichum alpinum*, *Lycopodium Selago*, *Streptopus amplexifolius*, and *Viola Selkirkii* have been collected only in rock ravines. From an ecological standpoint, however, it is the mass-effect of the vegetation rather than the occurrence of isolated species which is significant. Many of the bryophytes, which have already been referred to as being largely restricted to rock ravines in Connecticut, are much more generally distributed farther north. But even if these rock-face and crevice forms are ignored, the stamp of the north on the vegetation here is unmistakable. The predominant trees of ravine forests are usually species of northward range. The bryophytic flora of these forests—the mossy carpet of *Bazzania trilobata*, *Hylocomium splendens*, *Ptilium Crista-castrensis* and *Hypnum Schreberi* which frequently covers the forest floor—likewise is strongly suggestive of the north. In Sage's Ravine, and doubtless elsewhere, masses of *Sphagnum* grow high up on the slopes—a common phenomenon in the Maritime Provinces of eastern Canada. Moreover, in Connecticut, many vascular plants characteristic of the north woods, while by no means confined to this sort of habitat, attain their optimum development in rock ravines. As representative of this latter group of species may be cited:

Phegopteris polypodioides
Taxus canadensis
Streptopus roseus
Actaea rubra
Oxalis acetosella
Acer pennsylvanicum
Acer spicatum
Viola rotundifolia
Lonicera canadensis
Aster acuminatus

On the whole, the display of Canadian plants in rock ravines is noticeably richer than in any other sort of habitat, with the exception of bogs. Various explanations for this fact may be suggested. In the first place, the atmospheric conditions here are congenial to northern plants. As compared with less protected habitats, the air is more humid, while, especially in summer, the temperature is uniformly lower and less subject to extremes. Moreover, the length of the growing season is presumably shorter than in more open situations. In a Connecticut rock ravine there may thus be reproduced in miniature a type of climate similar to that which in the Canadian Zone prevails over vast areas. In the second place, geological factors are of undoubted significance. As has already been remarked, most rock ravines have remained practically unaltered since glacial times; they represent very ancient plant habitats. It seems probable, therefore, that boreal plants which today are confined to rock ravines may formerly have been much more widely distributed, and that they have been able to persist in their present habitats because of the unusually favorable environmental conditions there afforded. In the same way it is conceivable that the present boreal aspect of the vegetation in rock ravines may be reminiscent of a one-time much more universal aspect of vegetation in this region.

RAVINES IN UNCONSOLIDATED ROCKS

The unconsolidated stony materials which form so considerable a portion of the superficial crust of the earth are not commonly designated as rocks. "Yet no line of separation can be drawn between such solid rocks as those into which the sands and muds of distant geological ages have been transformed and the semi-consolidated deposits of more recent times, or the sediments now accumulating."* In the present paper, the term UNCONSOLIDATED ROCK embraces any uncompacted rock formation, such as sand, gravel, and clay. For the sake of convenience, the word ROCK itself, written without a qualifying adjective, is used in its popular sense to include only consolidated rock formations.

Distribution, Character, and Vegetation of Ravines in Unconsolidated Rocks.—In Connecticut, ravines of this description are by no means uncommon. They are developed along streams throughout the Central Lowland, while in the Highlands they may occur wherever there are deposits of glacial drift. More often than not they are relatively small and correspondingly unimpressive; but in some cases, particularly in the northern half of the Central Lowland, they may assume considerable size and importance.

---

* Barrell, J. & Loughlin, G. F., Conn. State Geol. and Nat. History Survey, Bull. 13: 17. 1910.

One of the best examples which the writer has examined of a ravine in unconsolidated rock is located in the town of Windsor. It has been scoured out to a depth of perhaps thirty feet from a coarse, sandy substratum through the activity of a small brook which flows into the Farmington River from the north. The slopes of the ravine, forested with hemlock, yellow birch, sugar maple, beech, white ash and tulip, contrast sharply with the surrounding upland which is largely overgrown with white pine, oaks, and chestnut. The undergrowth includes many of the herbaceous and shrubby species which have been listed as characteristic of rock ravines. But along with these grow *Lycopodium obscurum*, *Oakesia sessilifolia*, *Corylus americana*, *Geranium maculatum*, *Chimaphila umbellata*, *Pyrola rotundifolia*, and *Erigeron pulchellus* —all plants of relatively dry, open woods. As might be anticipated, the bryophytic flora is poorly represented. The rock-face and crevice mosses and liverworts, which constitute such a striking feature of the vegetation in rock ravines, are absent. Along the wet, sandy banks of the stream are a few species, such as *Pellia epiphylla*, *Conocephalum conicum*, *Mnium hornum*, and *Catharinaea undulata;* but aside from these about the only bryophytes present are a few forms which grow on rotten wood or humus, such as *Mnium cuspidatum*, *Stereodon cupressiformis* and *Georgia pellucida*.

Ravines in unconsolidated rock compare neither in scenic nor botanic interest with rock ravines. To be sure, all gradations are found between extremely shallow and scarcely perceptible depressions, which ordinarily would hardly be classed as ravines, and ravines of considerable depth, with fairly steep sides, like the one at Windsor. As a result of the diversity in environments which it is obvious may thus be afforded by different ravines, all stages of transition may be found between the vegetation of swamps and uplands on the one hand and that of typical ravines on the other. On the average, however, ravines in unconsolidated rock are smaller in size and are relatively broader and shallower than rock ravines. In consequence, the atmospheric conditions are seldom as favorable as those of rock ravines, and the vegetation rarely equals that of rock ravines in the high degree of mesophytism attained. Soil moisture, as a rule, would seem to be more important here in its effect on vegetation than atmospheric humidity. The boreal tone which characterizes the vegetation of rock ravines is likewise lacking. This would naturally be expected, not only on account of the less congenial environmental relations but also because of the comparative recency with which ravines in glacial deposits have been developed.

Spring Brooks.—As Cowles* has remarked, "springs and spring brooks may be classed with ravine streams, but differ from them in the relative absence of erosion phenomena." They might equally well, if not better, be classed with spring swamps,† with which they are usually associated. Spring brooks are common throughout Connecticut. Perhaps their most familiar floristic feature is the fringe of alders (*Alnus rugosa, Alnus incana*) which almost invariably lines their banks. Aside from these, the brookside flora may include any of the species elsewhere cited as characteristic of spring swamps.

The Succession of Vegetation during the Development of Ravines in Unconsolidated Rocks.—In his treatment of the plant societies of the Chicago region, Cowles‡ has described the development of clay ravines and the concomitant sequence of plant associations. The following observations are quoted from this work: "Wherever there is an elevated stretch of land adjoining a body of water, such as a lake bluff, one is apt to find excellent examples of the beginning of a ravine. *Fig. 1* [reproduced in this paper as FIG. 4] shows an embryonic ravine of a type which may frequently be seen along the clay bluffs. . . . A ravine of this type is essentially a desert, so far as plant life is concerned. The exposure to wind and to alternations of temperature and moisture is excessive. The lack of vegetation, however, is due chiefly to the instability of the soil; this instability is particularly great in the case of clay bluffs, where the seepage of water causes extensive landslide action.

---

* The physiographic ecology of Chicago and vicinity. Bot. Gaz. **31**: 98. 1901.

† See Bull. Torrey Club **42**: 192, 193. 1915.

‡ *Op. cit.*, pp. 86–88.

No plants can yet get a foothold in such a place, unless it be a few species that may be able to make their appearance between periods of landslide action; among these plants annuals particularly predominate. The perennials that may be found in such places are almost entirely plants which have slid down the bank. Ravines of a similar type may be seen in many places inland, and wherever found the poverty of vegetation on the slopes is the most striking character.

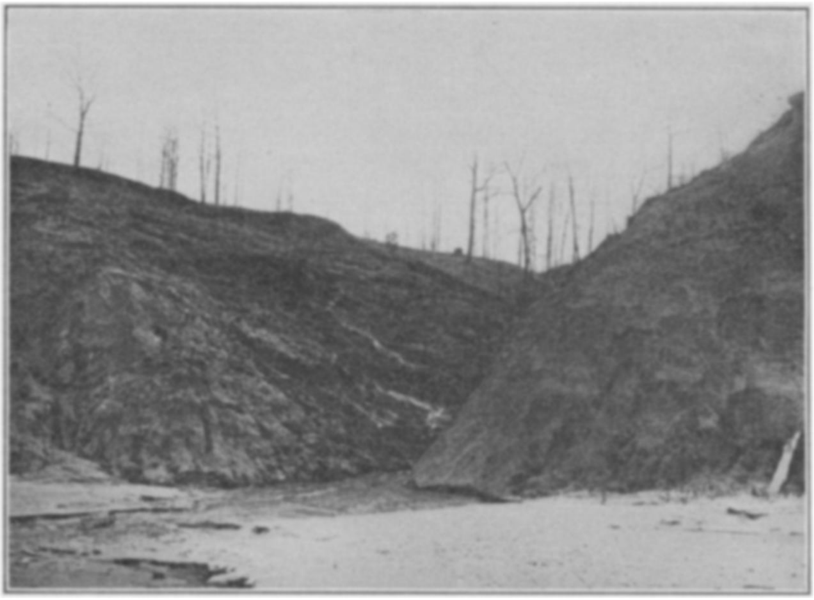

FIG. 4. An embryonic ravine in a clay bluff along the western shore of Lake Michigan. Vegetation entirely absent on the unstable clay slopes, except for shrubs and grasses which have slid down from the top. (After Cowles, Physiographic ecology of Chicago and vicinity; photograph furnished by H. C. Cowles.)

"As the ravine extends itself inland the conditions outlined above may be always seen about its head, but toward the mouth of the ravine the slopes are less precipitous. Torrents cut down the bed of the ravine until a depth is reached approaching the water level at its mouth. From this time on the slopes become reduced and the ravine widens more than it deepens, by reason of lateral cutting, landslide action, and side gullies. After a time a sufficient stability is reached to permit a considerable growth of vegetation.

If the erosion is slight enough to allow a vegetation carpet to develop, a high degree of luxuriance may be attained. In fact, ravine conditions are usually extremely favorable for plants, after the initial stages have passed. In a comparatively few years the vegetation leaps, as it were, by bounds through the herbaceous and shrubby stages into a mesophytic forest, ... Nothing shows as well as this the brief period necessary for a vegetation cycle in a favored situation as compared with an erosion cycle."

In Connecticut, clay ravines are much less frequent than are those in rock. They exist on a small scale in many parts of the Central Lowland, especially along the Connecticut River from Glastonbury to Windsor Locks, but elsewhere they are rare. Nowhere in this state are the successive changes in vegetation which accompany the development of a clay ravine so clearly shown as in the area described by Cowles, an area which the writer has visited on several occasions. So far as it has been possible to compare, however, the observations recorded in the Chicago region seem quite applicable to conditions in Connecticut.

PRE-EROSION TOPOGRAPHY AND ITS BEARING ON THE PHENOMENA OF SUCCESSION IN ROCK RAVINES

"From the standpoint of dynamic plant geography our land areas are divided into two well-marked categories: on the one hand is the erosion topography which is characteristic of the eroding and depositing phases of present streams and shores, and on the other hand is the preërosion topography which is characteristic of those areas that have not as yet been invaded by erosive forces."* To this latter category, speaking from the standpoint of the succession of plant associations, belong rock ravines. For while it is conceivable that, just as in the case of clay ravines, the topographic changes which accompany the development of rock ravines might react on the vegetation, yet such changes are brought about with such extreme slowness that their effect on plant life may be regarded as practically negligible. Whatever changes in the nature of ravine vegetation may have taken place in the past have probably been associated not only with topographic changes but with climatic changes as well; and the same will very likely hold true in the future. From a standpoint of present-day plant geography, therefore, the climax vegetation of rock ravines may be looked upon as practically permanent.

---

* Cowles, H. C. Bot. Gaz. **51**: 172, 173. 1911.

Although the fact cannot be overlooked that ordinarily the plant societies of rock ravines are associated with a definite phase of stream development, it should also be recognized that while very commonly the formation of a ravine has been due to the activity of streams which are still operative, this is by no means always the case. There are many rock ravines whose formation cannot be accounted for by contemporaneous factors at all. Often, as in the Devil's Gulch, the streams now present in such ravines can have played little part in their formation. Many streams have been superposed, so to speak, on the topography. They have found rather than made their channels. Not infrequently, as in the Wolf Den, ravines have been developed in other ways than by stream erosion. It is largely due to the prevalence of this preërosion type of topography, which has been moulded by physiographic forces of the geologic past, that rock ravines are so much more highly developed in the Highlands than in the Lowland.

RIVER AND STREAM BLUFFS

The later phases in river activity may be observed along most of the larger streams throughout the state. As the result of lateral cutting, the ravine once present has been replaced by a broad valley. As a ravine widens out, the exposure to wind, sun, and changes of temperature increases, and the moisture content of the slopes is appreciably modified. The effect of these environmental changes on vegetation can be seen by comparing the flora of a river valley with that of a ravine. In a general way, the vegetation of stream valleys can be treated under two heads: BLUFFS and FLOOD PLAINS. The term Bluff, as used here, includes not only the relatively steep slopes which frequently demarcate the valley from the upland, but also the gentler slopes which commonly occupy most of the intervening valley floor. In other words, it embraces all parts of the valley which, in contrast to flood plains, have been formed by erosion rather than by deposition.

The Vegetation of Bluffs in Unconsolidated Rocks.—In the

Chicago region,* the increased exposure which follows the widening out of a clay ravine may have a disastrous effect on the ravine flora.

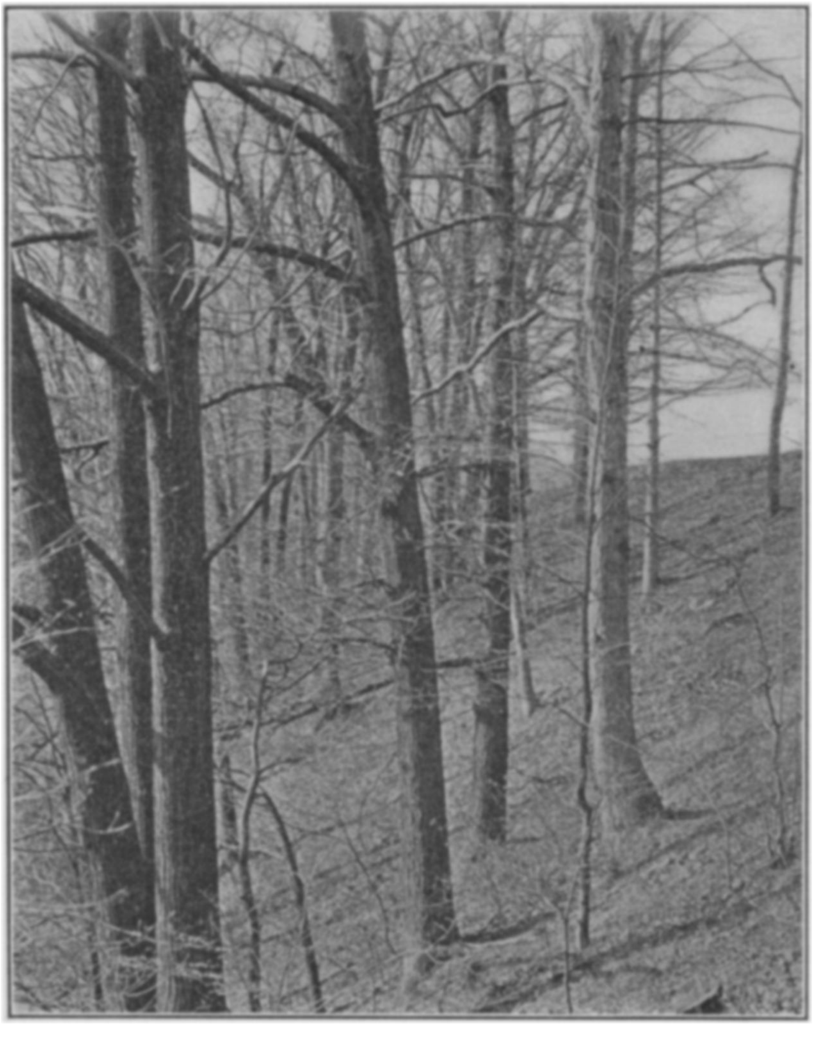

FIG. 5. Forest of chestnut, white oak, red oak, etc., along a sandy bluff bordering West River, New Haven. Elsewhere along the bluff, hemlock, beech and basswood are more or less abundant.

"The rich mesophytic herbs, including the liverworts and mosses, dry up and die, . . . and a xerophytic undergrowth comes in. . . .

---

* See Cowles, H. C., 1901, *op. cit.*, pp. 90–93.

After a few years have passed, xerophytic shrubs appear, . . . and it is not long until xerophytic or semi-xerophytic thickets prevail in place of the former mesophytic undershrubs. The last of the mesophytes to die are trees, because they are longer-lived than herbs and shrubs, and also because their roots reach down to the moisture"; but eventually these too give way to relatively xerophytic species. In Connecticut, the changes are not so radical; in fact, a bluff forest may be scarcely less mesophytic than a ravine forest. This is not surprising when it is considered that the climax formation in this region (that is, the most mesophytic type of vegetation which is capable of development on uplands) is very nearly as mesophytic as the climax association (termed by Cowles a "temporary climax") of ravines. In the Chicago region, on the other hand, the contrast between the mesophytic ravine forests and the xero-mesophytic climax forests on uplands is very pronounced.

The most striking difference between a bluff forest (Fig. 5) and a ravine forest is seen in the greater abundance of relatively intolerant trees. The undergrowth also, while it may contain any of the characteristic ravine species, includes many forms which ordinarily do not thrive under the shadier ravine conditions. On bluffs in unconsolidated rock, especially on clay and till, the soil moisture relations usually favor the continuance of a mesophytic flora. Near the mouth of the Windsor ravine, to select a concrete example, along the bluffs which border the Farmington Valley, common trees are *Juglans cinerea*, *Tilia americana*, *Betula alba papyrifera*, *Ulmus americana*, *Platanus occidentalis*, *Carya cordiformis*, *Quercus rubra*, *Ostrya virginiana*, and *Carpinus caroliniana*. Along with these occur the trees of the ravine forest—the sugar maple, white ash, tulip and yellow birch, and to a less extent the hemlock.

The undergrowth of moist valley forests is particularly rich in spring-flowering species. Among the herbaceous plants characteristic of such habitats may be mentioned the following:

Aspidium noveboracense
Asplenium Filix-femina
Adiantum pedatum
Osmunda Claytoniana
Botrychium virginianum
Oakesia sessilifolia
Allium tricoccum
Erythronium americanum

Asarum canadense
Claytonia virginica
Thalictrum dioicum
Anemonella thalictroides
Smilacina racemosa
Polygonatum biflorum
Medeola virginiana
Trillium erectum
Hepatica triloba
Anemone quinquefolia
Caulophyllum thalictroides
Sanguinaria canadensis
Dicentra cucullaria
Dentaria diphylla
Dentaria laciniata
Viola pubescens

The Vegetation of Rock Bluffs.—In comparing rock bluffs with rock ravines, one striking dissimilarity concerns the bryophytic flora. Species inhabiting the rock-face or the crevices, together with certain of the forest-floor species, may be well represented, but most of the others are absent. Under favorable circumstances a rock bluff may support a highly mesophytic vegetation; much apparently depends on exposure and on ground-water relations. Along the Connecticut River, south of Middletown, the north-facing bluffs are (or were) well forested; most of the vascular plants already cited as characteristic of rock ravines grow luxuriantly; *Acer pennsylvanicum* is common, attaining a height of more than thirty feet; and the mesophytic ravine mosses are well represented. The vegetation on the south-facing bluffs across the river, however, especially as regards the herbaceous flora, is much less mesophytic. In general, north- or east-facing bluffs are more mesophytic than those which face south or west. As might be expected, the highest degree of mesophytism prevails toward the bottom of a bluff; toward the top the vegetation is more xerophytic. In some cases, where the water supply is insufficient, mesophytes may be virtually lacking and xerophytes predominate from top to bottom. On the whole, the vegetation of the rock bluffs which border stream valleys throughout the state resembles that which has been described elsewhere* as characteristic of talus slopes.

Flood Plains

The topographic changes which take place during the building up of a flood-plain are accompanied by a fairly definite succession of plant associations. In the earlier stages of flood plain development, the surface of the ground is so low that it is covered with water at all seasons of the year. Here the vegetation consists of aquatic or semi-aquatic plants. As the surface is built up higher, it reaches a level where it is exposed to the air during summer, the period of low water, and here aquatic plants are replaced by terrestrial herbs. As the constructive process continues, the surface is built up to a height where it is out of water much of the year, and finally it may attain an elevation where it is out of reach of all but the highest floods. On these older flood plains grow shrubs and trees.

---

* See Torreya **14**: 181–184. 1914.

Flood Plain Associations along the Connecticut River.—Flood plains are formed to some extent along every sizable stream. In Connecticut, as might be expected, they are developed on the largest scale along the Connecticut River. Here, on the higher flood plains from Middletown northward, the rich alluvial soil furnishes the most fertile farm-lands in the state. As the result of agriculture, much of the primitive vegetation has been obliterated,* but it may still be seen to advantage on various flood plain islands (FIG. 6) and elsewhere. On an island at Windsor, in particular, the natural vegetation has never been disturbed. Whether or not it is true, as old residents maintain, that this island —now about three-quarters of a mile long, perhaps a hundred yards wide, and rising to a height of more than a dozen feet above low water level—has been developed entirely within the last thirty years, it is certain that it is growing rapidly at the present time, having increased several hundred feet in length at the lower end since it first came under the writer's observation in 1910. The following notes on the vegetation of the Connecticut River flood plains are based partly on the study of this island, partly on studies made at Middletown, Haddam and other points along the river.

As compared with a lake-swamp succession, free-floating aquatics, for obvious reasons, are rarely represented in a flood plain succession. The pond-lilies also are usually absent. Commonly the first forms to appear are submersed species, such as the pondweeds (*Potamogeton* sp.), *Vallisneria spiralis* and *Elodea canadensis*, which may grow in water four or even more feet in depth. In shallow water various aquatics with aerial foliage are ordinarily conspicuous. Of these, the following species are perhaps the most noteworthy:*

---

* Many of the grassy meadows along the Connecticut date back to pre-colonial days. It is recorded that when the first settlers arrived these areas were open and under cultivation by the Indians, who were accustomed to burn them over annually. But from the fact that today trees occur along the sloughs and scattered through the grassland, wherever they are permitted to grow, it would seem probable that these meadows were formerly forested, and that, if left to themselves, they would soon revert to their original condition.

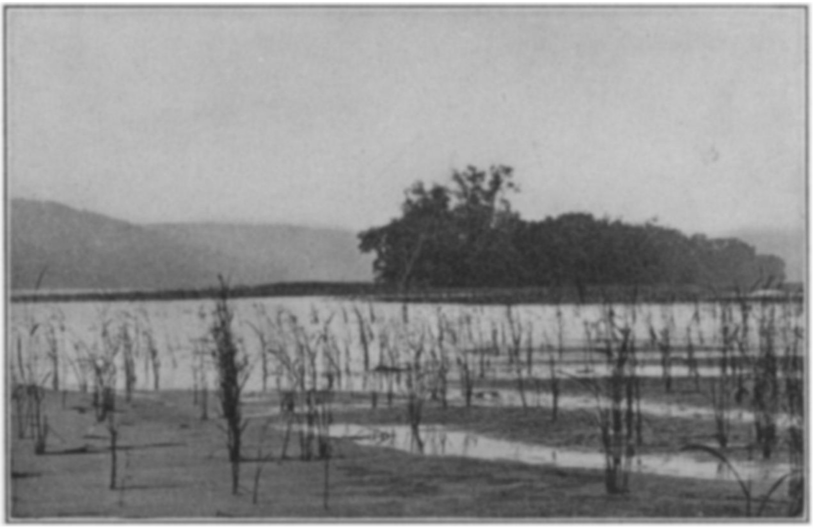

FIG. 6. Flood plain island in the Connecticut River, at Haddam. The plant in the foreground is the wild rice (*Zizania palustris*).

Equisetum fluviatile
Typha latifolia
Sagittaria latifolia
Zizania palustris
Scirpus americanus
Scirpus validus
Peltandra virginica
Orontium aquaticum
Pontederia cordata
Polygonum Muhlenbergii

While the number of species present at this early stage of flood plain development is relatively small, any lack of variety is more than counterbalanced by the luxuriance with which these few forms often grow. Fringing zones of pickerel weed and the like are quite as characteristic of flood plains as of lake shores, while marshy swamps, predominated by wild rice (FIG. 7) and other grass-like plants, are a prominent feature of many low flood plains, particularly toward the mouth of the river. Here, within the sphere of tidal influence, the ground occupied by these plants may be submerged at high tide and bare at low tide.

---

* From this and the two following lists have purposely been omitted a number of species which, while peculiar to the Connecticut River flood plains, seem too rare or too local to be of importance in the present connection. The majority of such species, so far as known, have already been mentioned elsewhere (Torreya 13: 106. 1913).

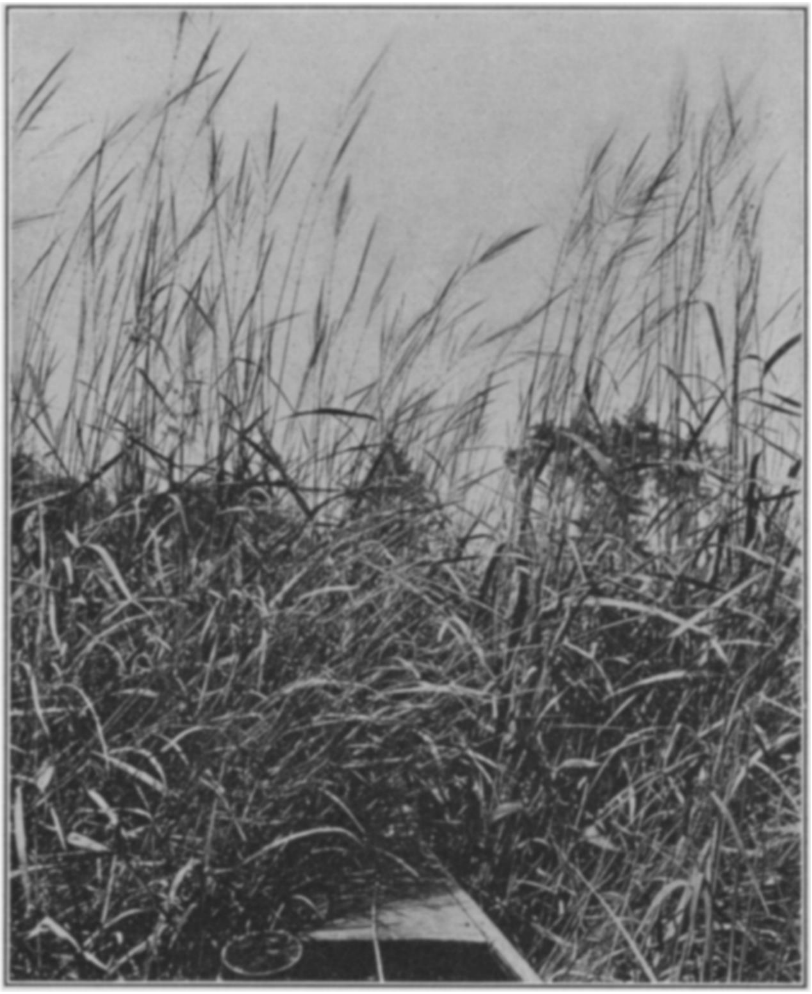

FIG. 7. Wild rice along banks of the Quinnipiac River, North Haven. Some idea of the height of this grass is suggested by the bow of the canoe in the foreground.

The second phase of flood plain development may well be designated the Strand Stage (FIG. 8). The surface of the ground is exposed for a longer or shorter period during summer, but is covered with water during winter. Certain algae, such as *Vaucheria* and *Botrydium*, are common here, as are also ephemeral bryophytes, such as *Riccia*, *Ephemerum*, and *Physcomitrium immersum*. The predominant vascular plants are either annuals or herbaceous perennials (or biennials)—forms which are able to develop between successive periods of submergence. On the lower, muddier parts of the strand, species with more or less pronounced amphibious proclivities may be well represented: such, for example, as *Echinochloa Walteri*, *Eleocharis aciculare*, *Penthorum sedoides*, and *Ludvigia palustris*. A list of other species characteristic of the strand stage is here given.

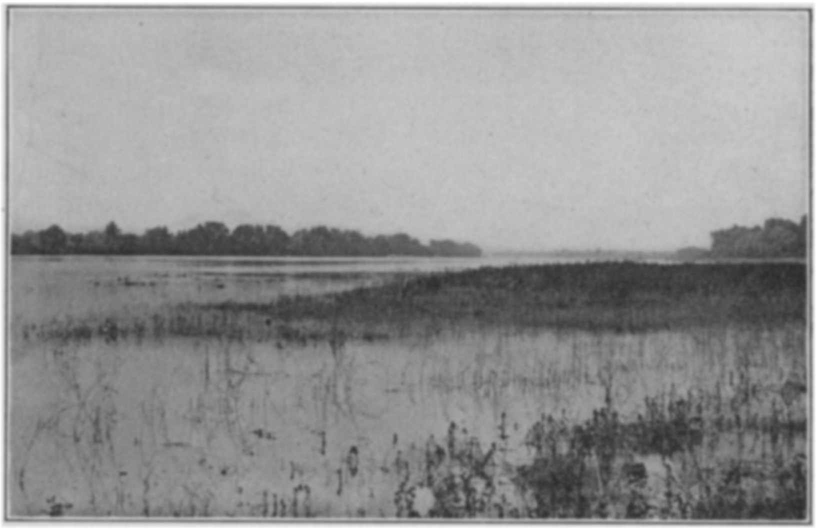

FIG. 8. A typical, low, flood plain strand along the Connecticut River, at East Windsor. Vegetation mostly herbaceous, but seedlings of willow and cottonwood abundant.

Equisetum arvense
Panicum agrostoides
Leersia virginica
Cyperus strigosus
Juncus effusus
Rumex crispus
Polygonum pennsylvanicum
Radicula palustris
Gnaphalium uliginosum
Ambrosia trifida
Xanthium echinatum
Bidens vulgatum

Woody plants are seldom wholly absent from the strand stage of a flood plain; commonly, seedlings of willow and cottonwood are abundant. Indeed, certain species of willow, such as *Salix cordata* and *Salix longifolia*, occur here which are usually lacking on older flood plains. But woody plants are rarely well developed; for even if they are able to withstand submergence in winter, trees and shrubs of any size are liable to be badly battered or else uprooted and carried away by the ice when it breaks up in spring. As soon, however, as the surface has been built up to such a height that it is beyond the reach of the winter ice, trees become the controlling element of the vegetation and ultimately a luxuriant forest may be developed. The boundary between the wooded part of a flood plain and the strand area is often marked by a distinct shelf or step—the result of ice-shove in winter.

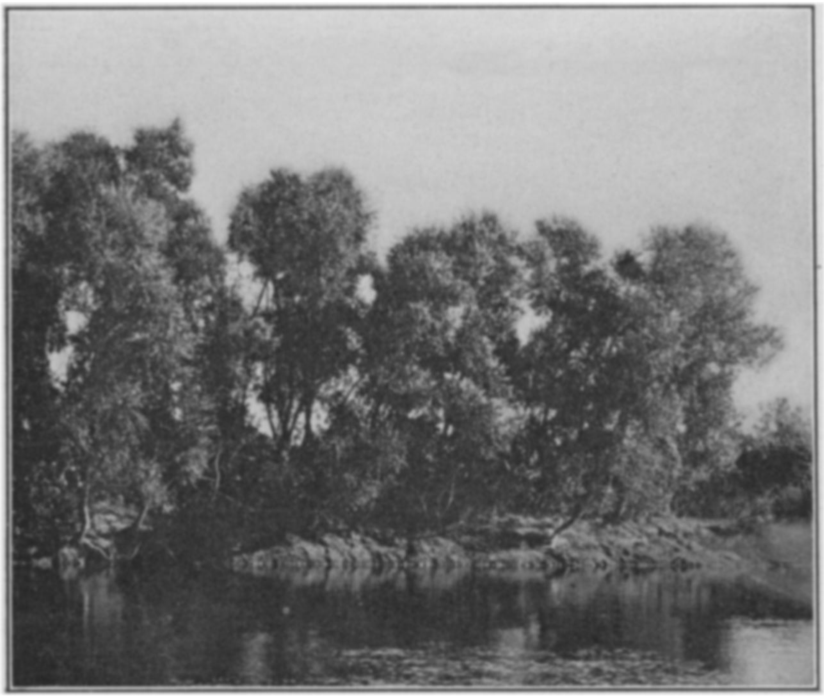

FIG. 9. Nearly pure growth of willow (*Salix nigra*) near southern extremity of flood plain island in Connecticut River, Windsor.

One of the first trees to establish itself on the flood plain is the black willow (*Salix nigra*). The willow is essentially a pioneer. Young flood plain forests (FIG. 9) may be composed almost wholly of this tree, while a zone of willow almost invariably fringes the shoreward margin of older forests. Closely following the willow, in fact often appearing simultaneously with it, are other trees, such as the sycamore (*Platanus occidentalis*) and the cottonwood (*Populus deltoides*), particularly the latter. As the surface of the ground continues to be built up higher, the soil becomes relatively drier and better aerated, so that conditions rapidly become less hydrophytic and more mesophytic. Under the changing conditions of soil and light, the willow gradually assumes a position of less and less importance, while the cottonwood comes to occupy a more and more prominent place in the rising forest (FIG. 10).

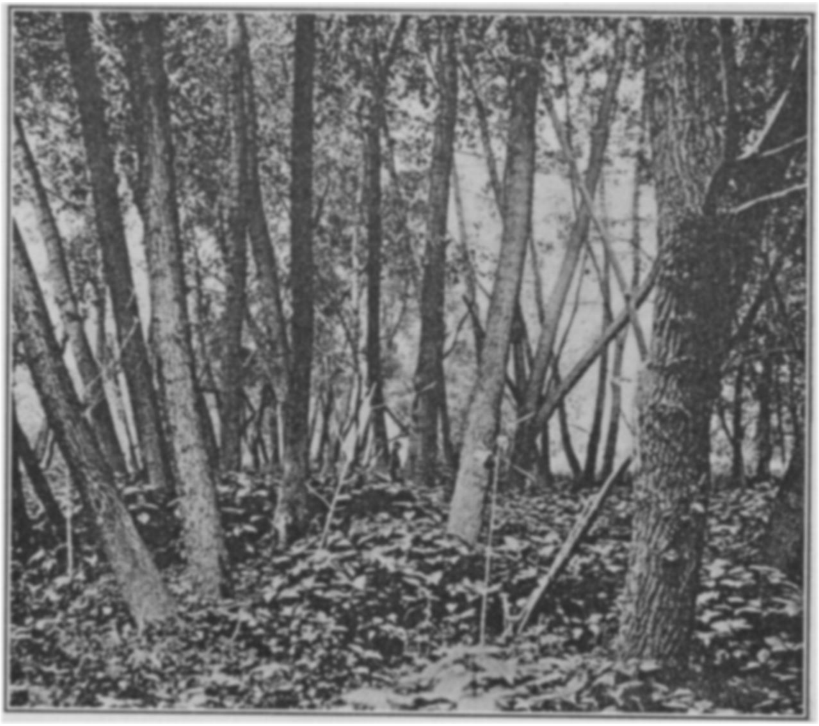

FIG. 10. Cottonwood forest with luxuriant herbaceous undergrowth (*Laportea*, etc.) on flood plain island at Windsor.

For while, like the willow, the cottonwood is relatively intolerant of shade, it grows more rapidly and to a much larger size, so that it tends to overtop and shade out the willow. Meanwhile other trees make their appearance. In addition to the species already enumerated, common trees on the Connecticut River flood plains are the elm (*Ulmus americana*), silver maple (*Acer saccharinum*), basswood (*Tilia americana*), white ash (*Fraxinus americana*) and red ash (*Fraxinus pennsylvanica*). Without exception, all of these last-named trees are more tolerant of shade than their predecessors. Springing up in the light shade which the cottonwood and willow produce, these more tolerant species become increasingly abundant until ultimately they dominate the forest. And while today the cottonwood and willow are perhaps the most conspicuous trees of the Connecticut River flood plains, there is little doubt that the forests which originally clothed the higher flood plains were made up largely of elm, silver maple, basswood, and ash.

A striking feature of the vegetation in flood plain forests is the wealth of lianas. Woody forms, such as *Rhus Toxicodendron*, *Vitis vulpina*, and *Psedera quinquefolia*, ascend the trunks of trees and hang in graceful festoons from the branches. A few herbaceous lianas also, notably *Sicyos angulatus* and *Echinocystis lobata*, clamber the trees, while numerous less vigorous species, *e.g.* *Polygonum scandens*, *Amphicarpa monoica*, *Convolvulus sepium*, *Solanum Dulcamara*, and *Clematis virginiana*, twine about or cling to any available support. The parasitic *Cuscuta obtusiflora* is a common form on the Windsor flood plain. Shrubs are usually few and scattered, about the only forms ordinarily present being *Cornus Amomum* and *Sambucus canadensis*.

The herbaceous undergrowth in such a forest is rank and luxuriant; some idea of its character is conveyed by FIG. 10. Tall, broad-, thin-leaved mesophytic plants predominate. The giant ragweed (*Ambrosia trifida*) commonly reaches a height of from ten to twelve feet, and the ostrich fern (*Onoclea Struthiopteris*), largest of the native ferns, a height of more than six feet. The nettles (*Laportea canadensis* and species of *Urtica*), growing more than waist-high, are uncomfortably abundant. Other characteristic herbaceous species worthy of mention are the following:

Asplenium Filix-femina
Onoclea sensibilis
Leersia virginica
Muhlenbergia mexicana
Cinna arundinacea
Bromus altissimus
Elymus canadensis
Pilea pumila
Boehmeria cylindrica
Thalictrum polygamum
Impatiens biflora
Viola cucullata
Circaea lutetiana
Verbena hastata
Eupatorium purpureum
Eupatorium urticaefolium
Solidago serotina
Aster paniculatus
Helenium autumnale

Flood Plain Associations along Other Streams.—The conditions described in the preceding paragraphs are found not only along the Connecticut, but also along the Housatonic and to a considerable extent along others of the larger rivers. But even along these rivers, there is a more or less noticeable variation in the aspect of flood plain associations, while along the smaller streams the departure from the described conditions may be very pronounced. On gravelly or stony flood plains, such as occur along swift streams, the pioneer forms of vegetation may be scraggly willows, alders,

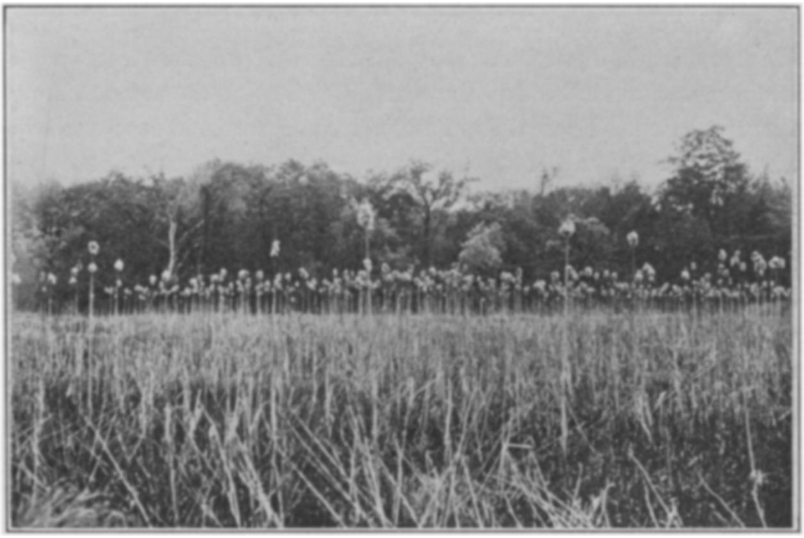

FIG. 11. Cat-tail (*Typha latifolia*) marsh along Muddy River, North Haven. In the background is a flood plain forest of elm, pin oak, etc.

and red-osier dogwood, along with which may grow a few herbaceous plants. Along many of the smaller streams throughout the state, during the building up of a flood plain, a sequence of plant associations is commonly encountered which is essentially similar to what has been described in an earlier paper* as characteristic of lakes and swamps. With the exception of the free-floating forms, any of the aquatic plants there mentioned may occur here. Of the species with aerial photosynthetic organs, the cat-tail (*Typha latifolia*) is especially conspicuous along many slow streams, frequently monopolizing wet, swampy tracts to the exclusion of practically everything else (FIG. 11). Marshes and meadows are quite as frequently developed along streams as along lake margins, and in general the aspect of the vegetation is similar in either case.† *Phalaris arundinacea* and *Leersia oryzoides*, however, might be mentioned as being more common in alluvial swamps than in other habitats. All of the shrubs and trees listed as characteristic of lake swamps are likewise found on flood plains along streams. Typical flood plain forests are best developed in areas which are subject to inundation only in spring. Here the soil relations are essentially those of a periodic swamp. Prominent trees in these forests along most streams are *Quercus bicolor* and *Quercus palustris*, species which are at least very infrequent in similar situations along the Connecticut. Except along the larger rivers, on the other hand, the cottonwood is practically absent and the silver maple is scarce. In addition to the two oaks already mentioned, the following trees are commonly represented in flood plain forests.

Carya cordifolia
Carpinus caroliniana
Ulmus americana
Liriodendron tulipifera
Acer rubrum
Tilia americana
Nyssa sylvatica
Platanus occidentalis

---

* Bull. Torrey Club 42: 176–194. 1915.

† Regarding the vegetation of Connecticut meadows in general it should be remarked here that while in the case of many wet meadows there seems to be no doubt that the present vegetation represents the original type, this is probably not true of all present-day meadow-lands. There is reason to believe that most of the less wet areas now occupied by meadow associations were formerly forested, and that their present vegetation has been developed only as a result of human interference with the original conditions. See footnote on p. 254.

Fraxinus americana *Fraxinus pennsylvanica*
Fraxinus nigra

The Temporary Nature of Flood Plain Forests.—It has been shown in the preceding pages that during the development of a flood plain the vegetation becomes less hydrophytic and more mesophytic, culminating in the formation of a mesophytic forest. Such a forest is to be regarded as the climax association of flood plains. But it can easily be seen that, owing to the activity of the river, this forest may be relatively short lived; in other words, it may represent only a temporary climax. For as the river meanders about on its flood plain in serpentine curves, it is constantly wearing away its banks on the outer, concave side of each bend, while at the same time deposition is usually taking place on the opposite, convex shores. In this way "a river may swing quite across its flood plain, destroying all that it has built, including the mesophytic forest."* Changes of this sort take place with appreciable speed and may be observed along almost any depositing stream.

Ox-bow Ponds.—In this connection should also be mentioned the crescent-shaped curves, or ox-bows, which are a characteristic feature of old-age streams. Frequently the meandering river shifts its course, abandoning a loop-like channel for a more direct route. The loop then becomes an ox-bow pond (FIG. 1, D), and as such its vegetation can best be treated with that of ponds and swamps.†

The Subsequent History of Flood Plains.—One other phase of river activity may be briefly sketched. It has already been shown that while deposition is the main feature of old-age streams, erosion is not wholly absent. In the course of time, for various causes, downward cutting may be renewed, the flood plains become terraces, and new flood plains may ultimately be formed at lower levels. The resultant topography is well illustrated along the Connecticut and others of the larger streams. The low flood plains of today are comparatively recent in origin. The more ancient flood plains are represented by sandy terraces, of which there may be one or more. These have attained their present condition through the downcutting of the rivers into the deep fill of glacial drift and outwash.* The effect of the changed topographic relations on these former flood plains as habitats for plants is readily comprehended. With the lowering of the river they must gradually have become more and more xerophytic and thus less and less tenable for the flood plain mesophytes. The actual effect of these changes on vegetation can only be conjectured. For, just as has been pointed out in the case of rock ravines, the period of time involved has been so great that oscillations in climate as well as changes in topography must presumably be taken into account. At the present day the vegetation of river and stream terraces is perhaps best treated with that of uplands, since the river has long since ceased to act as a dynamic factor in its development.

---

* Cowles, H. C., 1901, *op. cit.*, p. 107.

† See Bull. Torrey Club **42**: 171. 1915. *Fig. 1* of this paper pictures a typical ox-bow pond.

ACKNOWLEDGMENTS

For suggestions in connection with the preparation of this paper, the writer is greatly indebted to Professor Joseph Barrell, of the Geological Faculty, and Professor A. W. Evans, of the Botanical Faculty of Yale University, and to Mr. C. A. Weatherby, of East Hartford.

SHEFFIELD SCIENTIFIC SCHOOL OF YALE UNIVERSITY

---

* In this connection, see Rice, W. N., & Gregory, H. E., Manual of the Geology of Connecticut. Conn. State Geol. and Nat. Hist. Surv. Bull. 6: 35, 36. 1906.